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THE RELATIONSHIPS OF SEXUAL ORGANS IN PLANTS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXIII.

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THIS paper will attempt a classification of the sexual organs of plants based upon certain evolutionary principles and involving phylogenetic relationships in so far as these are understood. With the classification is presented a terminology new in certain respects and restricting some older names to a more precise significance. The establishment of a terminology is of course a matter of usage. The present suggestions are not offered through the desire to create a new set of terms, but rather as a means of making plain the fundamental characters of the classification. But there are some features which if adopted would lead to much greater clearness of expression.

Almost all of the sexual organs of plants fall into one of three groups, quite distinct from one another, each marked by fundamental characters so well defined that one form cannot pass into the other except through great changes of structure and behavior. The only sexual organs whose positions do not seem to be clear in this classification are the complex multicellular structures of the lichens and the Laboulbeniaceae. The conditions in these interesting forms are very puzzling, and much more must be known of their cell and nuclear structure and developmental history before we can hope to place them in relation to other forms. The three great groups of sexual organs in plants are:

I. *Unicellular structures developing uninucleate gametes.*—These organs may be called collectively *gametocysts* or, when sexually dif-

ferentiated, the male becomes the *spermatocyst* and the female the *oocyst*. They are restricted to the thallophytes and are generally characteristic of the algae, but are not the only types of sexual organs found in this assemblage.

II. *Multicellular structures developing uninucleate gametes.*— These organs comprise the antheridia and archegonia of the bryophytes and pteridophytes, which have probably been derived from a multicellular structure whose gametes were sexually undifferentiated (isogamous), which structure would be included under the more general term *gametangium*. In a harmonious terminology based upon the gametangium the male organ might be called a *spermatangium* and the female an *oangium*. Gametangia are represented among the thallophytes by the so-called plurilocular sporangia. Spermatangia (antheridia) are found in the Charales and Dictyota.

III. *Multinucleate sexual cells or coenogametes.*—These remarkable sexual organs, named by the author "coenogametes" (DAVIS '00, p. 307), are most typically illustrated in the Mucorales and Gymnoascales, but are also found in a somewhat modified form in the Saprolegniales, Peronosporales, and certain Ascomycetes. Coenogametes are morphologically either gametocysts that have become changed directly into gametes, or they are restricted portions of such cells.

These types of sexual organs will be considered in order, with a brief summarized list at the end of the paper.

I. GAMETOCYSTS, SPERMATOCYSTS, AND OOCYSTS.

The terminology which we shall use for the simplest sexual organs of plants (*unicellular structures developing uninucleate gametes*) is based upon suggestions of VUILLEMIN ('02) presented for the purpose of clearly separating this group from the multicellular reproductive organs characteristic of plants above the thallophytes. The unicellular sexual organ is well known to have had its origin from a reproductive cell which produced asexual spores, and such may be called a *sporocyst* consistently with the other terms. The list of unicellular reproductive organs leading to the high sexual conditions of the heterogamous algae, such as Volvox, Oedogonium, Vaucheria, the Cyclosporeae, and the Rhodophyceae, is then as follows:

Sporocyst, a unicellular structure producing asexual spores.
Zoosporocyst, a unicellular structure producing zoospores.
Gametocyst, a unicellular structure producing uninucleate gametes.
Spermatocyst, a unicellular structure producing sperms.
Oocyst, a unicellular structure producing eggs.

The terms sporangium, gametangium, antheridium, and oogonium, which have been applied to the above structures and to others as well, have been reserved for more precise usage, as will appear later in the paper.

It should be noted especially that this list includes the sexual organs of almost all of the groups of algae, forms which illustrate the usual course of sexual evolution. The principal stages and steps in the origin and evolution of sex are fairly well understood. The writer has recently described them (DAVIS '01, '03*a*) and will not take up the matter further than to emphasize some facts which have important bearings on the subject of this paper.

The gametocyst came into existence with the origin of sex, and was derived from a zoosporocyst whose zoospores became physiologically sexual. Sex has probably arisen a great many times in the plant kingdom, since it is fundamentally only a physiological condition, but so far as we know the origin has always been the same, namely through the conjugation of motile cells.

With the gametocyst established, there is sure to follow a tendency to differentiate the structure according as the sexual cells assume more and more the characters of sperms and eggs. The differentiation of sex is well known to be one of the results of plant evolution which has appeared in a number of divergent lines of ascent entirely independently of one another. The eggs and sperms of widely separated phyla in the algae, as for example those ending in Volvox, Vaucheria, Coleochaete, and Fucus, can only be related through their origin from the undifferentiated gametes or zoospores of a distant ancestry. So the mother-cells, oocysts, and spermatocysts of these sexual elements are related in the divergent lines among the algae only through an ancestry from the undifferentiated gametocyst or its progenitor the sporocyst.

There are several groups of algae which offer interesting peculiarities of structure that demand special explanations. In the filamentous Conjugales we have the union of gametes while still contained

within the cellulose walls of the gametocysts. This is far from a simple sexual condition, and it is a great mistake to present these types as illustrations of primitive sexuality. It is possible that the Conjugales have come by way of the unicellular forms related to the Volvocaceae, whose cells adopting quiescent habits gave rise to the desmids, through which the filamentous Zygnemaceae and Mesocarpaceae may have been derived. In many of the desmids the gametes escape from the gametocysts to fuse as naked masses of protoplasm. The retention in the Zygnemaceae and Mesocarpaceae of these gamete protoplasts within the gametocyst, and the consequent fusion of sexual cells surrounded by a cellulose wall is a peculiarity identical in this respect with the fusion of coenogametes in the Mucorales, Peronosporales, and lower Ascomycetes, and is evidence of a highly specialized sexual condition.

In the Rhodophyceae the spermatocysts have the peculiarity of producing each a single non-motile sperm, and the oocyst (carpogonium) develops a long filamentous receptive outgrowth, the trichogyne, surrounded by the cell wall, with which the sperm fuses. There is here, therefore, as in the filamentous Conjugales described above, the fusion of gamete protoplasts while still surrounded by their respective cell walls. Eliminating this peculiarity and the production of non-motile sperms, the sexual organs of the red algae appear to be similar to those of Coleochaete. There are some possibilities, however, which may complicate the problem of the classification of the sexual organs of the Rhodophyceae, and may relate it to the puzzling conditions in the Laboulbeniaceae and lichens. I refer to the presence of a trichogyne nucleus in Batrachospermum reported by myself, and the binucleate sperms described by SCHMIDLE ('99). We may find here and in other red algae peculiarities with direct relationships to the two fungal groups mentioned above.

The Charales present extraordinary conditions. The female organ is apparently an oocyst, surrounded, however, by a complex envelope of investing filaments; while the male organ is multicellular and consequently is not a spermatocyst, but falls within the second group of sexual organs, although it can hardly be supposed to have genetic relation to these. The spermatangium (antheridium) of the Charales is certainly one of the puzzles of plant morphology.

The male organs of some other algae, as Oedogonium, are groups of closely related cells which constitute a simple tissue, and similar conditions are also found in the Rhodophyceae, but all of these structures are really clusters of spermatocysts, and can scarcely be considered differentiated organs of the plants, even though they sometimes have very definite form. Nevertheless, the structures frequently are so constant as to have taxonomic value, and consequently probably always will be called antheridia in the works which deal with such matters.

The sexual organs of Dictyota present conditions that make their classification difficult. The cells producing male elements become divided (see figures of WILLIAMS '04) into a very large number of compartments, each of which develops a solitary sperm. This structure seems to be the same as that of the so-called plurilocular sporangia of the Phaeophyceae, in which case the male organs cannot be called sporocysts, but are true spermatangia (antheridia). The eggs, however, are formed singly in the mother-cells, which are therefore oocysts. The significance of these mixed characters in the group is not clear. Either the spermatangia (antheridia) are derived from spermatocysts that have adopted the peculiar methods of extensive cell division characterizing plurilocular sporangia, or the oocysts stand as the final stage in a remarkable reduction and final suppression of such activities in an ancestral multicellular female organ (oangium).

The desirability of some system and uniformity in the nomenclature of a group of reproductive organs which are clearly homologous (as are the sporocyst, gametocyst, spermatocyst, and oocyst) lies of course in the greater clearness and simplicity of the conception and expression of these relationships. The adoption of a new terminology for these structures will depend upon how strongly botanists may feel the need of these changes. Such old names as sporangium, gametangium, antheridium, oogonium, and ascogonium would be restricted to a narrower application, but, as we shall presently explain, they need not be entirely discarded.

It will be asked what are the particular advantages of the set of names proposed (sporocyst, gametocyst, spermatocyst, and oocyst) over older terms, and why have not the latter been retained and new

names proposed for the other great class of sexual organs, the multi-
cellular structures? The principal reason for the present suggestion
is the desirability of naming unicellular structures in a manner indica-
tive of their morphology. A better set of names would have been
sporocyte, gametocyte, spermatocyte, and oocyte, but the last two
terms have a special and precise significance in zoology. There is
no evidence of exact correspondence between the events of spermato-
genesis and oogenesis in animals and plants, but on the contrary
many reasons for believing that the processes have not only had an
independent origin, but have developed along quite different lines.
This subject cannot be treated at this time, but for these reasons we
have avoided the term spermatocyte and oocyte, and instead have
made use of VUILLEMIN'S suggest ons.

II. GAMETANGIA, SPERMATANGIA, AND OANGIA.

The second group of sexual organs comprises *multicellular struc-
tures which develop uninucleate gametes*. The fully differentiated
organs are best illustrated by the antheridia and archegonia of the
bryophytes and pteridophytes, but these heterogamous conditions
must have arisen from a simpler type of gametangium, and this must
be sought among the thallophytes. The writer (DAVIS '03) has
recently suggested their origin from a type of structure something
like that of the plurilocular sporangium of the Phaeophyceae and
the multicellular fruiting branches of such green algae as Schizomeris,
Stigeoclonium tenue irregulare, and the conditions sometimes found
in Draparnaldia and Chaetophora.

It will be difficult to displace such firmly established names as
antheridium and archegonium, but a terminology may be constructed
with sporangium and gametangium as a basis which is as consistent
and harmonious as that proposed for the first group of organs. It
would be as follows:

   Sporangium, a multicellular organ producing asexual spores.
   Zoosporangium, a multicellular organ producing zoospores.
   Gametangium, a multicellular organ producing uninucleate gametes.
   Spermatangium (antheridium), a multicellular organ producing sperms.
   Oangium (archegonium), a multicellular organ producing eggs (VUILLEMIN
        '02).

The origin of the sexual organs of the bryophytes and pterido-
phytes is necessarily a matter of speculation, but the relation that
they bear to one another and the type of structure which they repre-
sent are much more clearly understood than formerly.   These game-
tangia are essentially cellular capsules composed of an outer layer
of sterile cells which encloses a central mass of gametogenous tissue.
The development of the antheridium and archegonium generally
starts from a superficial cell, which by various divisions differentiates
a single terminal cell or a group of terminal cells that become the
growing points of the structure, building it up from above.   Thus the
antheridium and archegonium are from the beginning and at all
times tissues of a definite form whose cooperating cells establish the
organ.   They are not structures of the same class as certain assem-
blages of independent gametocysts whose cells are massed into definite
form, as for example many so-called antheridia of the red algae.

It seems to be perfectly clear now that the central region of cells
within the capsule wall of both antheridium and archegonium are
phylogenetically gametogenous tissues and are homologous; or,
expressed concretely, that the canal cells of the archegonium are
reduced and degenerate gamete mother-cells which together with the
fertile egg cell are homologous with the sperm mother-cells.   This
view, which has been held tentatively by many botanists for a long
time, is supported especially by observations by HY and TREUB,
and the recent studies of HOLFERTY and LYON.   GOEBEL ('02) in
an important paper has discussed the homologies of the sexual organs
in bryophytes and pteridophytes, recognizing that the suppression of
cell division and a process of sterilization were largely responsible for
the peculiarities of the female.   He also clearly showed the difficulties
that throw so much doubt on GÖTZ's theory of a relationship between
the archegonium and oogonium of the Charales.

HY ('84, p. 121) noted that various species of mosses present occa-
sionally the transformation of archegonia into antheridia, a phenome-
non apparently frequent in *Atrichum undulatum*.   TREUB's ('86,
pp. 107–108) observations on *Lycopodium Phlegmaria* are of the
greatest significance.   He found that the canal cells may contain two
nuclei, and he figures an archegonium in which a canal cell is divided
longitudinally so that the axial row is double at that point.   A dia-

gram which the author introduced to illustrate a theoretical stage
in the evolution of the archegonium (DAVIS '03 *c*, p. 491, *fig. 21, c*)
unwittingly almost duplicated this figure (TREUB '86, *pl. 21, fig. 9*),
to which his attention was called after the publication of this paper.
TREUB also noted the transformation of archegonia into antheridia
and archegonia whose tips remained closed and became abnormally
swollen. Recently HOLFERTY ('04) has determined for Mnium that
the series of canal cells is sometimes a double row for a greater or less
distance instead of the single line usually present, that the egg and
ventral canal cell are usually of nearly equal size, and that occasionally
organs are found with mixed antheridial and archegonial characters,
as when portions of an evident axial row break up into sperm mother-
cells. A number of observers have reported abnormalities among
the mosses, such as archegonia with two eggs, with two venters, or
with enlargements of the neck regions. These conditions all appear
to justify entirely the conclusions of the previous paragraph.

Especially interesting are some illustrations of unusual conditions
in the pteridophytes brought together by Miss LYON ('04). There
are the two canal cells that normally lie side by side above the ventral
canal cell of Equisetum, a condition also found in Isoetes. Two
eggs are occasionally present in the archegonium of *Selaginella apus*,
and a pair of eggs, one above the other with two canal cells between,
have been observed in *Adiantum cuneatum*. The most remarkable
conditions, however, are those found in *Lycopodium complanatum*,
whose deeply imbedded archegonia have sometimes as many as four-
teen to sixteen cells in an axial row, over half of which, and some-
times the egg cell itself, are binucleate. Thus the observations of
TREUB ('86) on *Lycopodium Phlegmaria* are substantiated, and it is
likely that others of the Lycopodiaceae have archegonia of a general-
ized type, with large amounts of potential gametogenous tissue.
They present conditions that may be expected in any primitive group
of bryophytes or pteridophytes. For male organs Miss LYON con-
tributes a new fact in finding submerged antheridia in *Lycopodium
annotinum*.

The evolutionary tendencies of antheridia and archegonia, from
their most generalized conditions among the bryophytes, are evidently
in the direction of numerical reduction of the number of gamete

mother-cells and the amount of sterile tissue developed. These tendencies are plainly shown in comparisons of the sexual organs of the pteridophytes with those of the bryophytes. The antheridia of the former group are all very much smaller than those of the latter; the wall of the capsule contains relatively few cells and the amount of spermatogenous tissue is very much reduced. Thus where thousands of sperms are developed in each antheridium of the bryophytes, there are less than a hundred formed in most of the pteridophytes, and sometimes very few (four in Isoetes). The archegonia of the pteridophytes have a smaller number of cells than those of the bryophytes. The neck region is much shortened and the number of canal cells becomes reduced from a large number in the bryophytes to two or three in some pteridophytes. Physiologically this reduction in the number of gametes, together with the greater specialization of egg and sperm, follows a history generally parallel with that in the thallophytes, and is what should be expected in any series of plants subject to the conditions that lead to the high levels of sexual evolution.

The history of the antheridium and archegonium in the reduced gametophytes of seed-bearing plants is not well understood, but this is not the time to discuss such difficult and highly special problems as the homologies of the stalk and body cell of the pollen grain or the egg apparatus and antipodals of the embryo sac. It is certain from the transitional conditions presented in the gymnosperms that the sperm and egg nuclei of the spermatophytes are homologous with the same gamete nuclei of the pteridophytes, and that they stand for antheridia and archegonia which have lost most and in some cases all of the sterile tissue characteristic of these organs as found in the bryophytes and pteridophytes.

With respect to the origin of the antheridium and archegonium, the investigations of HOLFERTY are strongly in support of the hypothesis previously suggested by the author (DAVIS '03 *c*). This hypothesis may be briefly summarized as follows: Since the antheridium and archegonium are multicellular structures from the beginning, and are morphological units developing from well-defined growing points, they cannot have been derived directly from the unicellular sexual organs (gametocysts) generally present in the thallophytes. They must have arisen from a multicellular structure (gametangium),

which was probably at the level of isogamy in its sexual evolution, because the gametogenous tissues in the antheridium and archegonium are essentially similar in structure, as is also true of the sterile tissue forming the surrounding capsule.   The only multicellular reproductive organs of the thallophytes which offer any possible points of relation seem to be the so-called plurilocular sporangia or gametang a of the Phaeosporeae, and similar structures in certain green algae, Schizomeris, *Stigeoclonium tenue irregulare*, and conditions occasionally found in Draparnaldia and Chaetophora.   Such multicellular reproductive organs of course must be regarded only as representatives of a certain type of structure (sporangium or gametangium), and not as direct ancestors of the sexual organs of bryophytes and pteridophytes.   I have never associated the archegonium closely with any individual form as Miss LYON ('04, p. 281) might lead one to suppose.

These sporangia and gametangia of the brown and green algae have the peculiarity that the original cells divide up into a great number of very small cells (loculi), each of which often develops but a single zoospore or gamete.   It is probable that the extensive cell division by which each zoospore or gamete is often given a separate compartment in the general structure is responsible for the origin of a multicellular reproductive organ (sporangium or gametangium) from some type of unicellular structure (sporocyst or gametocyst).   These sporangia and gametangia of the brown and green algae are known to be modified branches, generally somewhat smaller than vegetative branches.   Should such gametangia be placed under environmental conditions demanding protective coverings (as by a change from water to a land habitat), the first expression would be the sterilization of the outer layer of cells to form a protective capsule around the interior gametogenous tissue.   Such an advance would give the essential structure of an antheridium and an archegonium, and further specialization need be only along the well-known lines of sexual differentiation, by which one form of gametes would become somewhat modified as small sperms, and the other form, by loss of motility and through numerical reduction and consequent conservation of material for a few gametes, would become large eggs.   These matters have been discussed in full in the author's paper on "The origin of the arche-

gonium" (DAVIS '03 c) and the reader must be referred to that for
a detailed treatment of the subject.

Miss LYON ('04) has discussed the interesting problem of the rela-
tion of the sunken gametangia, characteristic of certain pteridophytes
(especially Lycopodium) and such liverworts as Anthoceros and
Aneura, to the stalked archegonium and to my theory associating
these structures with plurilocular sporangia.   She is inclined to derive
the sunken structure from an indeterminate region of gametogenous
cells which later might develop into an emergence with the general
characters of a gametangium (plurilocular sporangium).   This view
carries the origin of the archegonium still further back, and allows the
organ to develop through an emergent gametangium into the stalked
structure, or to remain partially or wholly imbedded in the tissues of
the gametophyte.   In the first group the archegonia would become
definite gametangia, comparable to plurilocular sporangia; while in
the second they would remain as less defined or indeterminate regions
of gametogenous tissue.   The chief difficulties in this view, in the
author's opinion, lie in the remarkable unity of structure displayed
by the archegonium, in the presence of a single terminal opening,
and the situation of the egg at the bottom of an axial row of gametog-
enous cells, which conditions imply an origin from some definite
type of gametangium whose fertile tissue was limited to a central
region.   The rarity among the known thallophytes of indeterminate
regions of gametogenous tissues present further important difficulties
in Miss LYON's theory.

Miss LYON ('04, p. 289), however, is inclined to pass lightly over
the latter difficulties, believing that transitory conditions may "be
readily found among the algae." She discusses several types and
presents a diagram of Ulva indicating a gametogenous tissue of
considerable thickness at the period of reproduction.   This is a very
deceptive diagram, for not only are there no walls formed between
the successive segments of protoplasm in the mother-cells, but the
latter are remarkably well-defined sporocysts, each independent of
its neighbors.   The membrane of Ulva is very far from constituting
a thallus several layers of cells thick, or even a differentiated tissue.
In Phyllitis there appears a successive segmentation of the protoplasm
within the mother-cells with the formation of walls by which the

zoospores or gametes are finally developed, each in its own compart-
ment, and this fact makes the group of cells derived from each mother-
cell a sporangium or gametangium.   The groups are quite independent
of one another and there is little hint of a tissue.   Essentially the same
conditions are found in Punctaria.   Porphyra is probably very similar
to Ulva in its methods of spore-formation, whatever may be the signifi-
cance of the so-called antherozoids and carpospores.   I am impressed
with the exceeding rarity in the thallophytes, and indeed in all plants,
of indeterminate regions of gametogenous tissue, and I know of no
form that illustrates clearly Miss LYON's conception of primitive con-
ditions such as she has tried to illustrate by her diagrams of Ulva.

Miss LYON might have made her case appear stronger on first
glance by citing Schizomeris and Pylaiella as illustrations of "inde-
terminate masses of reproductive cells."   In these two types the
sporocyst and sporangium or gametangium come so close together
that the general morphology of the respective fruiting filaments is
almost identical.   The distinctions, however, lie in the presence of very
numerous cell walls which are never found in sporocysts, and which
give the compartment structure to the sporangium and gametangium.

The development of cell walls following the segmentation of
protoplasm during sporogenesis may seem a very insignificant factor
on which to base a broad classification, but I think that close examina-
tion will prove it to be of fundamental importance, because the intro-
duction of these walls transforms a reproductive cell into a tissue,
however simple the arrangement may be.   I doubt if it is possible
to derive a clearly defined structure from the mere association of a
group of sporocysts or gametocysts, without the cell divisions indicated
above which immediately change the groups of reproductive cells
into sporangia or gametangia.   When a number of closely associ-
ated reproductive mother-cells divide in this manner, the tissue may
become quite extensive, and if these cells make up a well-defined
structure, as perhaps a filament or some emergent region, there is at
once developed an organ.   There are abundant illustrations of these
simple conditions, in various stages of relative complexity, in the
Phaeosporeae; for example the Ectocarpaceae present a wide range
from the generalized fruiting filaments of Pylaiella to the specialized
sporangia and gametangia (plurilocular sporangia) of Ectocarpus.

In this distinction of protoplasmic behavior during sporogenesis and gametogenesis (*i. e.*, the formation of cell walls during the segmentation of the protoplasm) lie the fundamental peculiarities of the sporangium and gametangium. And in this distinction are based my views of the homologies and origin of these structures. Associated with the peculiarity is the fact that sporangia and gametangia are almost universally superficial, and perhaps always have their origin from superficial cells. There may be exceptions to this general rule, as the antheridia of Anthoceros and some sunken sexual organs of the Lycopodineae, but these have not been sufficiently studied to justify conclusions. Thus, EMMA LAMPA ('03) has obtained Anthoceros plants bearing antheridia of superficial origin and regards these as representing primitive conditions, and one cannot guess what investigations among the pteridophytes may bring forth. The reasons for the superficial position of reproductive organs are probably at bottom physiological, although of course one may readily advance teleological explanations.

I do not find the same difficulty as Miss LYON in deriving the generalized and sunken sexual organs of some pteridophytes, notably the Lycopodineae, from superficial structures. Of course one does not relate them to extreme emergent types, such as are found in the Jungermanniales and Marchantiales. But a simple type of archegonium, sessile upon the gametophyte, might incorporate adjacent cells into its structure, especially if these are so generalized in character as to have reproductive potentialities, and thus become a more or less sunken structure. The emergence of an archegonium depends chiefly on the pushing out of a superficial cell, from which, so far as we know, the neck region is derived as from a growing point. And the egg in many sunken archegonia unquestionably takes its position because adjacent cells develop an uplifted portion of the gametophyte around it. Gametangia which are deeply sunken in the gametophyte, as in Lycopodium (and few have been reported), are perhaps as extreme in the direction of suppression as are the gametangia of mosses and most liverworts in the direction of emergence. These submerged sexual organs present difficulties that demand special investigation as to their origin. Thus, there may be an evolution of the sessile gametangium in both directions, on the one hand

leading to uplifted stalked structures and on the other resulting
in a submerged condition. We know at present too little of the com-
parative structure and development of the archegonium and antherid-
ium, to define safely the evolutionary tendencies throughout the
various groups of the pteridophytes.

III. COENOGAMETES.

Coenogametes (DAVIS '00, p. 307) are *multinucleate sexual cells*
and are morphologically either gametocysts that have become changed
directly into gametes or they are restricted portions of such cells.
Recent investigations have established their presence in various
Phycomycetes and Ascomycetes, and it is probable that future
studies will show them to be a type of sexual organ common in these
regions of the plant kingdom. We do not know enough to justify
speculation as to the exact relationships of these structures, but it is
not likely that they are all closely related to one another, and it is
very probable that various types of coenogametes may have arisen
independently.

Coenogametes fall into two classes: (1) those in which all of the
protoplasm of the parent cell is retained in the gamete; and (2) those
in which only a portion of the protoplasm is thus utilized, the remain-
der being devoted to other functions than that of reproduction. It
is not perfectly clear as yet whether the evolutionary tendencies are
from the first group towards the second or *vice versa*, or perhaps
irregularly both ways. But from our knowledge of the lines of sexual
evolution in the other two groups of sexual organs (gametocysts and
gametangia), the author believes the general advance to be from the
simpler first class of coenogametes to the more complicated second
class.

Coenogametes of the first class are best illustrated by the sexual
organs of the Mucorales and the Gymnoascales. The latter group
has been recently studied by Miss DALE ('03), who finds that the
earliest stage of the gamete is a uninucleate cell which becomes
multinucleate as it increases in size. After the union of these coeno-
gametes the ascogenous hyphae develop from a coiled prolongation
that grows out from the fusion cell. We do not know the history of
the nuclei in the fusing gametes of the molds or in Gymnoascus, but
there is every reason to expect that most of them unite in pairs, as is

the case under similar conditions in *Albugo Bliti* and Pyronema.   It is probable that the conditions in Gymnoascus will be found to be generally present in what are usually called the lower groups of the Ascomycetes.   It looks very much as though such genera as Eremascus, Eurotium, Ceratostoma, Sordaria, and Ascobolus will be found to present sexual organs essentially similar to those of Gymnoascus. Their general agreement with the sexual processes of the Mucorales may have great significance in connection with the origin of the coenogamete and possible relation of the Mucorales and Ascomycetes to one another or to a common algal ancestry.

Coenogametes of the second class are much better understood with respect to the details of protoplasmic structure and behavior than those of the first class.   The development of the sexual organs and processes of fertilization are perhaps as well known in Albugo (STEVENS '99, '01) and Pyronema (HARPER '00) as for any plant types.   In *Albugo Bliti* and *A. Portulacae* the ooplasm contains numerous nuclei, and an equally large number is introduced into the egg from the male coenogamete, these sexual nuclei then fusing in pairs.   Other species of Albugo (*e. g., A. Tragopogonis*) show a lessening number of functional and potential gamete nuclei in the egg, until forms are reached in *A. candida* and *A. Lepigoni* (RUHLAND '03) whose eggs are normally uninucleate.   This series in the genus Albugo, so well described by STEVENS ('01), is very interesting and we shall refer to it again. All other genera of the Peronosporales have, so far as is known, uninucleate eggs (Pythium, Peronospora, Sclerospora, and Plasmopara).   In Pyronema there is developed a conjugating tube that takes out of the female coenogamete many of its nuclei.   But a very large number are left in the structure, and these fuse in pairs with numerous male nuclei that enter the female cell by way of the conjugating tube.   The female coenogamete of Monascus, according to BARKER ('03), cuts off a sterile cell and thus disposes of some of its protoplasm. The recent discussion of IKENO ('03) as to the systematic position of BARKER's form deals with the life history after fertilization.   There is no criticism of BARKER's account of the structure of the sexual organs.   Although not positively established, there are good reasons for believing that the numerous gamete nuclei of Monascus fuse in pairs as in *Albugo Bliti*, *A. Portulacae*, and Pyronema.

The Perisporiaceae, Lichenes, and Laboulbeniaceae among the Ascomycetes present sexual organs of a highly differentiated character. These are very much specialized groups whose morphology and life histories indicate a degree of development and differentiation far above most of the simpler forms that we have just discussed (Gymnoascus, Monascus, Pyronema). The gametes of Sphaerotheca (HARPER '95, '96) are uninucleate, and it becomes an interesting problem whether or not this form stands at the end of a series representing nuclear reduction from a coenogamete, such a series as is illustrated by the species of Albugo. The recent studies of BAUR ('98, '01) and DARBISHIRE ('00) on the lichens have clearly established the sexuality of these forms and the significance of the ascogenous hyphae. But we do not sufficiently know the nuclear conditions to justify any extended speculations on the homologies of the cells in the archicarp and trichogyne of the female sexual organ. And similarly the sexual organs of the Laboulbeniaceae (THAXTER '96) present most interesting and puzzling complications of cell structure that cannot be explained until we know the detailed history of the nuclei in the processes of development and fertilization.

In a discussion of the origin and evolution of coenogametes much depends upon the relation of the structures in the first and second class. Which is the more primitive type? Some botanists will claim that conditions of the first class (Mucorales and simpler Ascomycetes) illustrate degeneration from h˙gher sexual forms. The author is of an opposite opinion, believing that the coenogametes of the first class illustrate closely the conditions of very simple and the most primitive types of coenogametes. This view has been discussed in a previous paper (DAVIS '03 b, pp. 233–327, and 331–339), but may be summarized briefly here.

The coenogametes of the first class are morphologically gametocysts which have given up the function of forming numerous gametes (represented by the many nuclei), but obeying chemotactic influences of a sexual character fuse with one another as coenocytic units. They would represent a relatively low level of sexuality (isogamy), and their progenitors would be looked for among groups whose gametocysts discharged motile gametes that fused in pairs, as is illustrated among the isogamous Siphonales. An ancestry of this

character under certain conditions, as through a change from aquatic to aerial habits, might give up the habit of developing motile sexual elements, which would be represented, however, by the numerous gamete nuclei fusing in pairs in the cytoplasmic union of the parent coenogametes. We have excellent illustrations of the sacrifice of motile spore-forming habits in the conidia of Peronospora and some species of Pythium, which germinate by a tube instead of developing zoospores. These conidia are morphologically sporocysts which have become coenocytic units, and coenogametes are gametocysts which have become coenocytic units. It must not be supposed that coenogametes are all related to one another. They might readily arise, according to our theory, from various types and at different times, thus making possible a number of developmental lines.

The coenogametes of the second class are restricted portions of cells, which like those of the first class are morphologically gametocysts. Indeed in many cases the mother-cell is essentially a unit, even though only a part of the protoplasm is actually the sexual element, because the remainder has some special relations or functions in connection with the sexual processes. Thus the periplasm of the Peronosporales and the conjugating tube of Pyronema hold such intimate relations to the sexual portion of the protoplasm that the entire gametocyst is really a coenocytic unit, and might be called the coenogamete instead of the restricted portion that is actually fertilized. From the conditions in the genus Albugo it would seem that some coenogametes of the second class follow the general law of sexual evolution, reducing the number of functional gamete nuclei until the eggs are uninucleate. The series from *Albugo Bliti* and *A. Portulacae* through *A. Tragopogonis* to *A. candida* and *A. Lepigoni* is a most interesting one, and the author (DAVIS '03 *b*, p. 323, 324) has already expressed his agreement with STEVENS and RUHLAND that the drift of development in the genus is plainly in the above order, from the multinucleate to the uninucleate egg. We may hope with increasing studies on the sexual organs of Ascomycetes to discover evolutionary lines in this group, but our knowledge is entirely insufficient at present to justify conclusions. Thus, uninucleate gametes like those of Sphaerotheca may represent the last stage in a process of nuclear reduction. And along a·very different line such

structures as conjugation tubes (Pyronema), accompanying sterile cells (Monascus), or an investing cellular envelope (Araiospora) might give rise to more conspicuous accessory structures.

It need not be supposed that coenogametes of the second class are all derived from those of the first class, and in some regions there are good reasons for believing that this has not been the case, especially since the processes of oogenesis in Vaucheria (DAVIS '04) conform in the most essential features with those of the Peronosporales and Saprolegniales. These three groups agree in the fundamental fact that extensive nuclear degeneration takes place in the gametocysts previous to the formation of the sexual cells. In Vaucheria all but one of the nuclei become disorganized. In Saprolegnia a number survive in relation to several coenocentra that determine the position of the eggs which are occasionally bi- and trinucleate. In the Peronosporales the surviving nuclei lie in the ooplasm, and when only one is selected it is because of close proximity to the large coenocentrum. These conditions in the Peronosporales and Saprolegniales are so similar to one another and to Vaucheria in various particulars that there are evident relationships, but whether these are direct or more general by way of a common ancestry among the lower Siphonales is a problem that perhaps may be better handled when we know more clearly the processes of oogenesis in such forms as Sphaeroplea, Monoblepharis, and some other types. Their processes of oogenesis are likely to conform to the type in Vaucheria.

Whatever may have been the origins of the several types of coenogametes representing the second class, problems which are very difficult and perhaps impossible to solve with the fragmentary evidence left to us, we can at least attempt to judge the probable direction of their development, and possibly establish some system or law of their sexual evolution. As stated before, some botanists will hold that even the simplest forms of coenogametes (Mucorales and Gymnoascales) have been derived from heterogamous algae by processes of simplification or degeneration. The author cannot take this attitude, believing as he does that the simplest coenogametes have had their origin from isogamous algae, that they may tend to pass into higher conditions leading to those of heterogamy, and that very much the same factors are at work to differentiate the sexual elements in this region of the plant kingdom as among the algae.

The old group of the Oomycetes has been a favorite starting point for evolutionary lines in the Ascomycetes and Mucorales. DeBary pointed out the resemblances between the Ascomycetes and members of the Peronosporales, and since his time a number of writers have traced lines of relationship with greater or less detail. The most recent expression, that of Barker ('03), considers Albugo as presenting sexual organs sufficiently primitive to be like the progenitors of the Ascomycetes. The less complicated sexual organs of Gymnoascus, Eremascus, etc., and the similar conditions in the Mucorales have very generally been regarded as derived from higher conditions (as in Albugo) by a process of simplification or degeneration, whereby sexually different gametes become essentially similar.

The two regions of the algae most discussed in attempts to establish points of origin of the higher Phycomycetes and Ascomycetes have been Vaucheria and the Rhodophyceae. The resemblances of Vaucheria to the Peronosporales and Saprolegniales are very striking, the more so since the recent studies in oogenesis have brought all groups into close sympathy. The author believes that that there are relationships here, although probably they are not direct. But when the Mucorales are annexed on the theory that the highly differentiated sexual organs of heterogamous groups may become generalized to those of the molds, then difficulties appear which seem at present insurmountable. There is no morphological evidence of such a line of development, and the process as a physiological event would be quite unparalleled and contrary to all known principles of sexual evolution. And similarly Barker's view that *Albugo Bliti* presents sexual conditions simple enough for the most primitive ascomycete does not seem to the author justified by its cell and nuclear activities (Davis '03 *b*, pp. 344, 345).

The remarkable resemblances between the Laboulbeniaceae and the Rhodophyceae have been noted by Thaxter ('96), who has suggested that the Ascomycetes may have arisen from this point in the plant kingdom. The similarity of the Laboulbeniaceae to the red algae is certainly very striking, and there are no more interesting problems in this region of plant morphology than those involving careful comparisons of the sexual processes and the development of the cystocarp and ascocarp in these two groups. There are indica-

tions among the red algae in the trichogyne nucleus of Batrachospermum and its binucleate sperms (SCHMIDLE '99) of conditions which if found more generally may assist to a clearer understanding of these remarkable fungal groups and materially support THAXTER's view.

It is very difficult to conceive a relationship between the sexual organs of the simpler Ascomycetes (Gymnoascales, etc.) and those of the lichens and Laboulbeniaceae.   One can scarcely conceive of a process of simplification by which the former could have come from the latter.   On the other hand, the general principles of sexual evolution operating upon the simple sexual organs of the lower Ascomycetes would be more likely to result in the conditions illustrated by Monascus, Pyronema, and Sphaerotheca than those of the lichens and Laboulbeniaceae.   Such an evolution would also be in sympathy with the general ascending complexity of vegetative thallus and ascocarps in the forms under consideration.   This view would place the progenitors of the simpler Ascomycetes in a region much lower than the Rhodophyceae, and perhaps relate them to certain Phycomycetes.   There is of course the possibility of the Ascomycetes being polyphyletic, removing the Laboulbeniaceae from the general assemblage, which might dispose of these difficulties, but we must know much more about the comparative development of the ascocarps in the groups before such a view can be considered well-founded.

The author cannot agree with any view that fixes the origin of the Mucorales and Ascomycetes from conditions illustrated by any known living form.   The problems of relationship involve so many considerations, those of taxonomy as well as evolutionary tendencies in sex, that arrangements of living types in series seems futile.   He believes that the most hopeful line of speculation will be founded on the close study of the principles of sexual evolution and a comparison of forms in this light, with such checks as may be furnished by the comparative morphology of all phases in the life history of the types.   And these principles indicate to the author much simpler primitive sexual organs for the Ascomycetes and Mucorales than have been supposed, and with their origin below the Peronosporales (Oomycetes), and perhaps finally, for the Mucorales at least, from the isogamous Siphonales (DAVIS '03, p. 335).

We cannot at this stage in the progress of investigations give a

precise statement of the evolutionary tendencies of coenogametes, but certain factors may be considered, of which the principal ones seem to be cooperative in both the Phycomycetes and Ascomycetes. Assuming that coenogametes may have arisen at various times independently of one another, and from an ancestry at approximately the level of isogamy or slightly above it, their evolution might proceed along three or more divergent lines. They all agree in having very numerous potential gamete nuclei, and there is strong evidence from the processes of gametogenesis in Saprolegnia, the Peronosporales, Pyronema, and Vaucheria that these are under conditions which demand extensive nuclear degeneration. Consequently the evolutionary tendencies are largely concerned with the disposition of superfluous nuclei and seem to present the following possibilities.

I. General nuclear degeneration may result in the survival of a few gamete nuclei in relation to coenocentra and the development of a limited number of eggs, as in the Saprolegniales.

II. Superfluous nuclei with some cytoplasm may be differentiated as a periplasm, with functions to perform in laying down portions of the spore wall, which conditions accompanied by numerical reduction of the nuclei in the ooplasm give the general tendencies in the Peronosporales. There is apparently presented in Araiospora (KING '03) a modification of the habits in the Peronosporales, since the periplasm in this form develops a cellular envelope around the spore.

III. In the Ascomycetes we have a much wider range of conditions, with proportionally much less knowledge of the forms, so that the working out of evolutionary lines becomes very speculative. However, superfluous protoplasm with nuclei is used here to form accessory structures, such as the conjugation tube of Pyronema and the sterile cell of Monascus. There is probably also numerical nuclear reduction, which would culminate in uninucleate gametes, as in Sphaerotheca. The multicellular trichogynes and archicarps of the lichens and the Laboulbeniaceae present some very difficult morphological problems, with possible relations, however, to conditions in the Rhodophyceae, especially should further study in the latter group establish the presence of multinucleate sexual organs.

The suggestions of the paragraph above must of course stand the test of extensive investigations on many more forms and with refer-

ence to points of general morphology as well as those that concern the
sexual organs alone.   The former would have been treated by the
author had they appeared to present difficulties in his views, but they
seem to be in general accord.   Thus the simplest types of coeno-
gametes are found in the simpler groups of Phycomycetes and
Ascomycetes, and the more complex conditions in forms above.

If coenogametes may lead up towards a heterogamous level of
sexual evolution, their sexual organs, while closely resembling those
of the algae, might not be strictly homologous.   Thus the eggs of
Saprolegnia and the Peronosporales do not seem to be the exact
homologues of the eggs of any alga, and the female organ is unlike
the typical oocyst because of obvious relations to coenogamete condi-
tions.   Their male organs differ from spermatocysts in their coeno-
cytic behavior.   Similarly the sexual organs of the Ascomycetes do
not fall into the classification based upon the gametocyst.   For these
structures the old designations of oogonia, ascogonia (archicarps),
and antheridia are applicable, and they will be thus distinguished
from the two main classes of sexual organs, the gametocysts and
gametangia.

IV.   SUMMARIZED LIST OF THE SEXUAL ORGANS OF PLANTS.

This summary presents the new terms introduced in our discussion
of the sexual organs of plants.   As stated in the beginning of the
paper, the establishment of a terminology is a matter of usage; its
importance will rest entirely on the value of the classification and its
ability to express the characteristics.   These new terms will interest
chiefly the morphologist who seeks to understand and express rela-
tionships.   Much of the work of taxonomy disregards difficult prob-
lems of morphology, and in this subject the older descriptive terms
(oogonium, antheridium, sporangium, etc., among the thallophytes)
are sure to be used, in some cases without regard to the exact homol-
ogies of the organs considered.

Sporocysts are unicellular structures developing asexual spores.

Gametocysts are unicellular structures developing uninucleate gametes.   These
are the most primitive types of sexual organs and are derived from *zoosporocysts*,
unicellular structures that develop zoospores.   Gametocysts become sexually
differentiated into

Spermatocysts, unicellular structures developing sperms, and

Oocysts, unicellular structures developing eggs.

Gametangia are multicellular organs which develop uninucleate gametes. These are believed to be derived from zoosporangia, multicellular structures which form zoospores. According to the author's hypothesis (DAVIS '03 *c*) the gametangia of groups of extinct Chlorophyceae leading into the bryophytes became differentiated into

Spermatangia (anther:dia), multicellular organs developing sperms, and

Oangia (archegonia), multicellular organs developing eggs.

Coenogametes are multinucleate sexual cells, and are morphologically either gametocysts that have become changed directly into gametes, or they are restricted portions of such cells. In the Mucorales and Gymnoasceae the coenogamete contains all of the protoplasm of the parent cell. In the Peronosporales and certain Ascomycetes only a portion of the protoplasm of the gametocyst is utilized in the gamete, the superfluous protoplasm passing into sterile structures (periplasm, conjugating tubes, sterile cells, etc.). The sexual organs of these latter forms, which are probably higher conditions than the former, may very properly retain the old names of oogonium, ascogonium, and antheridium. The structure of the sexual organs of the lichens and the Laboulbeniaceae is not sufficiently known to establish their position in this classification.

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